

A review of diets in the Notaspidea (Mollusca: Opisthobranchia)

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ABSTRACT

This paper reviews the scattered and often anecdotal literature on foods for the opisthobranch order Notaspidea. All Umbraculacea are sponge-feeders (accepting sponges of the class Demospongiae only). The Pleurobranchacea shows a diversity of diet: *Berthella* species eat sponges (Demospongiae); *Berthellina* species eat sponges (Demospongiae; ? Calcareia) and cnidarians (Scleractinia — not previously reported; ? Actiniaria); *Pleurobranchus* species eat ascidians; *Pleurobranchaea* (and apparently *Pleurobranchella*) species are opportunistic carnivores that accept a range of soft-bodied invertebrates (Cnidaria; Annelida; Mollusca). It appears that cnidarians (Actiniaria; Hydroida) are amongst the more preferred items in the diet of *Pleurobranchaea* species. The review is supplemented with observations on feeding of *Berthellina citrina* (Rüppell & Leuckart) and *Pleurobranchaea maculata* (Quoy & Gaimard) made at Leigh, New Zealand.

INTRODUCTION

Investigations on nutrition in opisthobranchs are few in comparison to works on their taxonomy. However, studies on the feeding habits of species of the more advanced orders (Notaspidea, Anthobranchia (= Doridacea), and Nudibranchia *sensu* Minichev, 1970), all of which are carnivorous, are appearing gradually. Recent studies build upon the classical works on aeolids (Braams & Geelen, 1953; Steehouwer, 1955). There have been some sophisticated (laboratory and field) studies recently on dorids (Potts, 1970; Elvin, 1976; Seed, 1976; Perron & Turner, 1977; Nybakken & Eastman, 1977; Barbour, 1979; Eyster & Stanyck, 1981) and aeolids (Morse, 1971; Harris, 1973; 1975; Harris *et al.*, 1975; Edmunds, 1975; Edmunds *et al.*, 1974; 1976; Christensen, 1977; Conklin & Mariscal, 1977; Day & Harris, 1978; Rudman, 1979; 1981a; 1981b; Hall *et al.*, 1982). McDonald & Nybakken (1978) have presented a thorough summary of the diets of Californian nudibranchs. Research on the Notaspidea lags far behind. The majority of observations on food and feeding available for members of this order in the literature are by-products of taxonomic studies. Some observations appear paradoxical at present, but there is a long way to go and surprises can be expected.

Since the Anthobranchia and Nudibranchia probably evolved from the Notaspidea (Odhner, 1939), or at least through a "pleurobranch grade" of organization (Minchev & Starobogatov, 1978; Willan, 1983), the Notaspidea is significant when considering

overall evolution of feeding patterns in the Opisthobranchia. An understanding of food types and nutritional physiology amongst the Notaspidea is also important in tracing evolution within the nudibranchiate orders. In fact there are many parallels in feeding biology between anthobranchs and pleurobranchs.

The order Notaspidea has two suborders — Umbraculacea and Pleurobranchacea. The Umbraculacea contains one family (Umbraculidae) with three genera — *Umbraculum* Schumacher, *Tyrodina* Rafinesque, *Tyrodinella* Mazzarelli (Odhner, 1939; Pruvot-Fol, 1954). There are no studies specifically on feeding for any umbraculacean. The Pleurobranchacea also contains one family (Pleurobranchidae) with two subfamilies and eight genera (Pleurobranchinae — *Pleurobranchus* Cuvier, *Berthella* Blainville, *Berthellina* Gardiner, *Pleurehdera* Marcus & Marcus, *Bathyberthella* Willan; Pleurobranchaeinae — *Pleurobranchella* Thiele, *Pleurobranchaea* Meckel in Leue, *Euselelops* Pilsbry) (Willan, 1983). Detailed accounts of food or feeding are those on *Pleurobranchus membranaceus* (Thompson & Slinn, 1959), on *Berthellina citrina* (Usuki, 1969; Marbach & Tsuramal, 1973), on *Berthella plumula* (Delaloi & Tardy, 1977) on *Pleurobranchaea californica* (Chivers, 1967; Lee et al., 1974) and on *Pleurobranchaea maculata* (Ottaway, 1977b).

Moquin-Tandon (1870), Vayssi re (1883) and MacFarland (1966) have given accounts of the structure of the alimentary canals of *Umbraculum mediterranea*, *Tyrodina citrina* and *Tyrodina fungina* respectively. The gut of the Pleurobranchidae has been described by Lacaze-Duthiers (1859), Vayssi re (1898), Guiart (1901) and Thompson and Slinn (1959). The alimentary canal, which is stereotyped throughout the latter family, is almost unique amongst opisthobranchs in possessing a single, dorsal accessory gland (the "acid gland") that produces a strongly acidic secretion (Thompson & Slinn, 1959; Kandel, 1979). The structure of the extrinsic buccal muscles of the Pleurobranchidae was covered by Brace (1977) in his broader study of the muscular anatomy of the cephalopodal mass and accounts of the intrinsic buccal musculature have been presented by Bergh (1898), Hoffmann (1939) and Marcus and Marcus (1957). The mode of operation of both sets of buccal muscles and their nervous co-ordination has been investigated experimentally by Davis and Mpitsos (1971), Davis et al. (1973) and Lee and Liegeois (1974).

This paper compiles and assesses the widely-scattered data on notaspidean diets and is augmented with personal observations made in (particularly) New Zealand and Australia. Each genus of the order is considered separately in this review because there is hardly any overlap between references from one genus to the next. The work concludes with a summary on feeding relationships within the order Notaspidea.

REVIEW

Tyrodina and *Tyrodinella*

Notaspideans belonging to these two small genera are exclusively sponge feeders. They eat sponges belonging to the class *Demospongiae and, in fact, all sponges identified hitherto as foods belong to a single order (Verongida) and family (Aplysinellidae). The European *Tyrodina perversa* feeds on *Aplysina crassa* [previously called *Verongia aerophoba*] (Haefelfinger, 1962; Boury-Esnault, 1971; Ros, 1975). The Californian *Tyrodina fungina* eats *Aplysina fistularis* [previously *Verongia thiona*] (Ricketts & Calvin, 1939; Lance, 1961; Sphon & Mulliner, 1972; Ros, 1975; Nybakken, 1975; Farmer, 1980; Beeman & Williams, 1980); actually Behrens (1980) claimed *T. fungina* subsisted exclusively on this one sponge. *Tyrodinella spongotheras*, a Canadian species, was found on *Aphrocallistes vastus* (class Hexactinellida, Dictyonina), the interstices of which were filled with *Aplysina* sp. (Bertsch, pers. comm., 1979; Bertsch, 1980).

The Australian *Tyrodina corticalis* also feeds on aplysinellid sponges. Of the four *Tyrodina corticalis* I have collected live, two were together on the aplysinellid *Pseudoceratina* sp. and had obviously been eating it (pers. obs., 18 m, Julian Rocks, northern New South Wales, 30 Jan. 1983). Coleman (1975: 100) recorded that this

* Higher classification for sponges follows Bergquist, 1978; 1980.

Australian species ate sponges exclusively and provided a coloured illustration of a specimen *in situ* on a massive orange sponge belonging to the family Thorectidae (order Dictyoceratida). It is not known if the *Tylodina* was actually eating this sponge; if so *Tylodina corticalis* may have a slightly broader dietary range than its congeners.

Umbraculum

All references indicate that species of this genus (of which there are probably no more than two throughout the world (Thompson, 1970)) feed on sponges, although the particular poriferan taxa are not usually specified (Moquin-Tandon, 1870; Graham, 1955; Abbott, 1974; Ros, 1975; Coleman, 1975: 103; Coleman, 1981: 64).

The taxa of sponges now known to be accepted as food by *Umbraculum* are notably more diverse than those eaten by the previous two genera. And it is interesting that sponges belonging to the orders Verongida and Dictyoceratida are entirely absent from those presently recorded as food for *Umbraculum* species.

Coleman (1975: 102; 1981: 63) provided coloured illustrations of *Umbraculum sinicum* *in situ*; in each case the animal was on top of a massive sponge — presumably its food. The sponge depicted in the latter figure belongs to the Spirastrellidae (Hadromerida).

As part of her field studies on subtidal sponge ecology at Leigh, New Zealand, Ayling (1978) observed *Umbraculum sinicum* feeding on five demospongiid sponges: *Tethya aurantium*; *Tethya ingalli*; *Aaptos aaptos* (Hadromerida, Tethyidae); *Ancorina alata* (Hadromerida, Stellettidae); *Plakina trilopha* (Homosclerophorida, Plakinidae). From personal observations at the same locality I can add *Tethya amplexa* (Hadromerida, Tethyidae) to Dr Ayling's list, and I have also witnessed *U. sinicum* eating *Ancorina alata*. In addition, Ayling (1978) tracked a single *U. sinicum* for 18 months and during that period it ate specimens of four different sponge species.

Umbraculum sinicum appears not to wholly consume its sponge food (Ayling, 1978; pers. obs.) but it does cause extensive damage (Fig. 1). Coleman (1981) reported *U. sinicum* to eat "entire colonies [of sponges] down to the base". *U. sinicum* devours the inner layers of tethyid sponges to leave merely a hollow ball of cortical tissue.

Species of the Umbraculidae do not have a protrusible pharynx, so the food must be brought in direct contact with the mouth which is located in a cleft at the anterior end of the foot (Willan & Morton, 1984).

Berthella

There is a dearth of information concerning diet for members of this large and widespread genus. The only detailed study is that by Delaloi and Tardy (1977) on *Berthella plumula*. This pleurobranch feeds at night on the sponge *Oscarella lobularis* (Demospongiae, Homosclerophorida, Oscarellidae), excluding all other sponges and ascidians found in the same environment and tested as possible food. The observations were repeated by Bouchet *et al.* (1978). Pruvot-Fol (1954) and Ros (1975) reported three Mediterranean species of *Berthella* to feed on sponges and other molluscs. I have found spicules belonging to *Plakina monolopha* (Demospongiae, Homosclerophorida, Plakinidae) in the faeces of *Berthella ornata* from New Zealand.

Thompson and Slinn (1959) and Yonge and Thompson (1976) surmised *Berthella plumula* [and *Berthellina engelii*] fed on compound ascidians because that is the diet of the only other British pleurobranch — *Pleurobranchus membranaceus*.

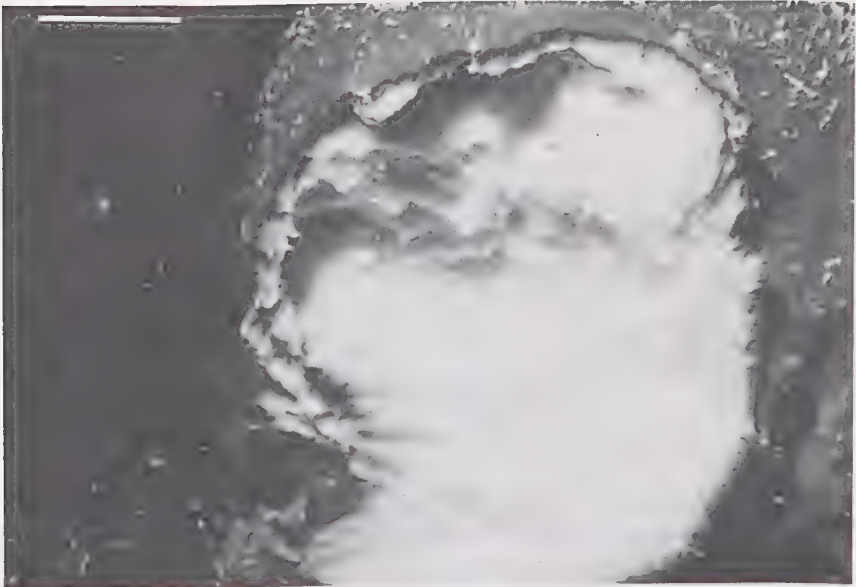


FIG. 1. Illustration shows a large sponge (*Ancorina alata*) from which an *Umbraculum sinicum* that was feeding had just been removed. Note how the sponge's tissues have been hollowed out by the slug. Photographed in 17m, "Sponge Garden", Leigh Marine Reserve New Zealand, J.M. Dollimore, 22 March 1978. Scale bar represents 1cm.

Berthellina

Marcus and Marcus (1967: 44) cited the observations of Professor F.M. Bayer that *Berthellina quadridens* ate sea anemones in the laboratory. Further evidence of the food of *Berthellina* species comes from faecal analyses. On this basis, Marbach and Tsumamal (1973) inferred *B. citrina* was a sponge feeder; spicules belonging to species of Demospongiae (*Myriastris purpura*, *Desmacella* sp., *Biemma* sp., *Mycale* sp., *Damira schmidtii*, *Callyspongia crassa*) and even Calcarea (*Sycon* sp.) were identified. Hill (1963) recognised sponge tissue and numerous broken sponge spicules in the stomach of *B. citrina*. Thompson (1977) concluded *Berthellina quadridens* was also a sponge feeder.

Several authors have reported algal material in the gut of *Berthellina* species (Gohar & Abul-Ela, 1957; Usuki, 1969; Marbach & Tsurumal, 1973). Marbach and Tsurumal (1973) also found minute crustaceans and calcareous spicules from a didemnid ascidian in the gut of *B. citrina*. Macnae (1962) reported finding partially digested shrimps in the stomach of two *B. citrina*. These unlikely plant and animal remains were probably ingested accidentally along with the principal food.

Mr Scott Johnson has very generously permitted me to include his (largely unpublished) observations on feeding of *Berthellina citrina* in Hawaii in this review. He found this pleurobranch, which is nocturnal, to feed not only on sponges (*Terpios zeteki* (Demospongiae, Hadromerida, Suberitidae), *Leucetta solida* (Calcarea, Leucettida, Leucettidae) and an unidentified red encrusting sponge) but also on three species of corals (*Tubastrea coccinea* (Scleractinia, Dendrophyllidae), *Porites lobata* (Scleractinia, Poritidae) and *Leptastrea purpurea* (Scleractinia, Faviidae)) (Johnson, pers. comm., 1979; 1980). Mr Johnson has published a magnificent coloured photograph of a *Berthellina citrina* feeding on *Tubastrea coccinea* (Bertsch & Johnson, 1981: 26) and most generously permitted me to reproduce that illustration in this review (Fig. 2).



FIG. 2. *Berthellina citrina* eating the coral *Tubastrea coccinea*. Photographed at night in a cave in 8-12 m, Puako, Hawaii. S. Johnson, May 1978. Extended crawling length of slug 45 mm. From Bertsch and Johnson, 1981.

Considering the abundance of *Berthellina citrina* in Hawaii, the incidence of coral feeding appears to be low (Johnson, pers. comm., 1980). Mr Johnson has observed *B. citrina* feeding most frequently on *Tubastrea coccinea* (on more than 20 separate occasions). Observations have been made at the following locations: Puako (Hawaii Island); Yokohama and Pupukea (Oahu Island). All observations were made at night in depths between eight and ten metres. These are the first authentic records of a pleurobranch eating scleractinian corals.

Whilst collecting pleurobranchs for taxonomic studies at the University of Auckland's marine field station at Leigh, New Zealand (36°16'S; 174°47'E) from 1974 to 1979 I often

observed *Berthellina citrina* feeding in the field and conducted some preliminary investigations on the diet of this pleurobranch in the laboratory (Willan, 1975). *Berthellina citrina* spends the daytime resting in depressions on the undersurfaces of stones that lie on clean sand or shell gravel; at night animals emerge in search of food. *B. citrina* cannot be induced to feed in the light under any circumstances. Animals consistently display a strong negative phototactic response (Strasburger, 1879) when crawling or feeding activity is interrupted by the beam of an underwater torch. Bertsch (1970) has described an identical light avoidance response in *B. engeli* from North America, and Marbach and Tsurumal (1973) have also reported the nocturnal behaviour of *B. citrina* in the Red Sea.

Spicules from four tetractinomorph demospongiid sponges were identified from the faeces of field-collected *Berthellina citrina*; these sponges were *Ciocalypta polymastia*, *Hymeniacion hauraki*, *Raspailia* sp. and *Suberites* sp. However, these faeces had been treated with dilute nitric acid (according to a method recommended by Dr P.R. Bergquist, and routinely employed by sponge workers) so remains of calcareous sponges or other soft-bodied invertebrates would not have been detectable. In the laboratory, *Berthellina citrina* that had been starved for 48 hr or longer, consumed the following ten sponges: *Tethya aurantium*; *T. deformis*; *Halichondria moorei*; *Ciocalypta polymastia*; *Microciona coccinea*; *M. rubens*; *Iophon minor*; *Damira* sp.; *Coelosphaera calcifera*; *Tetrapocillon novaezelandiae*. The *Halichondria moorei*; *Iophon minor*, *Damira* sp., *Tethya deformis* and *Tetrapocillon novaezelandiae* were almost completely devoured, the other five to a lesser extent. Four other sponges were offered, but were not eaten: *Cliona celata*; *Ciocalypta polymastia*; *Hymeniacion spherodigitata*; *Clathrina* sp. These qualitative results show that *Berthellina citrina*, even at a single locality, has a broad dietary range and will (presumably preferentially) select sponges belonging to the orders Hadromerida, Halichondrida and Poecilosclerida of the Demospongiae. Preliminary laboratory tests indicate *B. citrina* locates its food by chemotactic behaviour.

Usuki (1969) reported that captive *Berthellina citrina* readily accepted squid meat. None of my experimental animals, however, would touch meat.

Bathberthella* and *Pleurehdera

No information is available concerning food for either species of these two monotypic pleurobranch genera. This is because the former is only known from deep water (>1600m) and the latter is presently known from only a single specimen.

Pleurobranchus

The fullest account of feeding by a member of this genus is the study by Thompson and Slinn (1959) on *Pleurobranchus membranaceus* in England. That species ate ascidians in the laboratory; both solitary and compound forms being accepted readily. *P. membranaceus* drilled through the test of larger solitary ascidians (e.g., *Ascidia mentula*, *Ascidia aspera*) and ingested colonial ascidians whole (e.g., *Botryllus schlosseri*) (Thompson & Slinn, 1959; Thompson, 1976; Thompson & Brown, 1976; Yonge & Thompson, 1976). Yonge (1949) observed *P. membranaceus* waiting beside a contracted ascidian with its oral tube poised above an unopened siphon. As soon as the ascidian opened, the *Pleurobranchus* plunged its proboscis in to eat the soft viscera. This diet of ascidians is reported in almost every general account of *P. membranaceus* (Hunt, 1925; Hyman, 1967; Morton, 1979).

Remains of ascidians have been found in the gut of several *Pleurobranchus* species: *P. grandis* and *P. mamillatus* (Vayssi re, 1898); *P. ovalis* (Thompson, 1970); *P. grandis* (Marcus & Marcus, 1970); and *P. evelinae* (Thompson, 1977). Ros (1975) quoted Vayssi re's earlier report of *P. testudinaria* feeding on ascidians. MacFarland (1966) (repeated by Nybakken, 1975) inferred *P. strongi* fed on compound ascidians because it was regularly found on or near these organisms. Thompson (1977) suggested that it would be unlikely for the North American *P. areolatus* to feed on anything but ascidians because all of its congeners possess that diet.

The only authors to report any food for *Pleurobranchus* species apart from ascidians were Marcus and Marcus (1963). They found "masses of Globigerinae" in the stomach of *P. areolatus*.

Pleurobranchaea

There is more literature on food and feeding biology for species belonging to this genus (especially *Pleurobranchaea californica*, *P. maculata* and *P. meckelii*) than any other in the Notaspidea. Species of *Pleurobranchaea* are notorious for their carnivorous habits. Beeman and Williams (1980) reported that *P. californica* was often taken on set lines and in crab pots. Captive specimens will devour raw meat, squid or fish (Mestayer, 1920; pers. obs., 1974), other opisthobranchs (Burn, 1957; 1966a: 107; 1966b; Harris, 1973; Chamberlain & Behrens, 1980; Beeman & Williams, 1980), smaller specimens of their own species (Bergh, 1897; Hirsch, 1915; Pruvot-Fol, 1927; Marcus, 1957; Coan, 1964; Chivers, 1967; Beeman & Williams, 1980), or their own spawn (Davis *et al.*, 1974a; Truman, 1978). Hirsch (1915) mentioned this cannibalistic habit; one *P. meckelii* (41 gm) examined by him had a 27 gm specimen in its stomach. Sometimes *Pleurobranchaea* species are cannibalistic in nature as Marcus and Marcus' (1957: 24) observations attest. Nowadays *P. californica* is maintained routinely in the laboratory, solely on a diet of raw squid meat (e.g., Lee & Palovcik, 1976; Davis *et al.*, 1977). Coan (1964) cautioned that behaviour exhibited by animals in captivity might not be a good indicator of the behaviour of the species in nature.

Compilation of observations on food types derived through gut analyses from field-collected specimens produces a bewildering array of potential foods. Vayssi re (1901) found remains of two species of thecate hydroids in the gut of *P. maculata*. Marcus and Marcus (1966) recovered hydroids, caprellids and other amphipods from *P. gela*; they found hydroids, polychaetes and crustaceans in *P. occidentalis* (Marcus & Marcus, 1967); and they recovered a polychaete from *P. hedgpethi* (Marcus & Marcus, 1969). Chamberlain and Behrens (1980) found the following items in the gut of *P. californica*: opisthobranch molluscs; isopods; copepod exuviae; fish scales; "transparent tunicate-like organisms".

Starm hlner (1968) claimed *Pleurobranchaea meckelii* ate ascidians and sponges, and Schmekel (1968) suggested this species fed on other opisthobranchs (both were repeated by Ros (1975)).

It can be certain that *Pleurobranchaea* species are opportunistic carnivores. They are voracious feeders and forage actively. Live food seems to be preferred to dead material. Hirsch (1915) (quoted by Hyman, 1967) is the only author to suggest *Pleurobranchaea* species scavenge dead organisms; according to him *Pleurobranchaea meckelii* "roams the bottom for corpses which it detects only by contact". Apparently, almost any soft-bodied invertebrate is vulnerable to attack and ingestion. *P. maculata* will attack (see later description of feeding behaviour) organisms with protective shells (e.g., gastropods, bivalves, crustaceans), but it cannot ingest them. Similarly *P. californica* will not swallow the spicule-containing dorid nudibranch *Aegires albopunctatus* (Harris, 1973). Such foods as are acceptable would be taken according to their abundance at a particular time or to a preference on the part of the *Pleurobranchaea*.

It appears that cnidarians are some of the most preferred items in the natural diet of *Pleurobranchaea* species. This view arises in part from the reports of Vayssi re (1901) and Marcus and Marcus (1966; 1967). Support comes from observations made by Moore (1964), Chivers (1966), Harris (1973), Ottaway (1977a; 1977b) and Beeman and Williams (1980). Moore (1964, quoted in Garlo, 1977) noted *P. tarda* on floating *Sargassum* sp.; this alga would be very likely to harbour hydroid colonies. Chivers (1967) witnessed an attack by a large *P. californica* on a medium-sized *Anthopleura elegantissima* (Actiniaria, Actiniidae); the pleurobranch almost completely devoured the sea anemone in less than ten minutes. Harris (1973) observed that *Pleurobranchaea* [presumably *californica*] readily attacked anemones. Beeman and Williams (1980) reported that *P.*

californica ate *Anthopleura elegantissima*. Ottaway (1977a) listed *P. maculata* as a predator of *Actinia tenebrosa* (Actiniaria, Actiniidae). Ottaway (1977b) subsequently gave more details, based on laboratory trials, of the method of attack of *P. maculata* on this actinian (see Figs. 3 and 4). He recorded that one *P. maculata* (90mm in length) was capable of eating 100 *A. tenebrosa* in three and a half days. Ottaway's findings led him to conclude predation by *P. maculata* could be an important biological factor in restricting *A. tenebrosa* to the intertidal zone (Ottaway, 1977b).

FIGS. 3, 4. *Pleurobranchaea maculata* eating an actinian (*Actinia tenebrosa*).



FIG. 3. Animal making a feeding lunge at the anemone; note protracted lips and buccal mass, cupped oral veil and forward-directed rhinophores.



FIG. 4. Animal feeding on the anemone's column. Photographed in an aquarium, Edward Percival Marine Laboratory, Kaikoura, New Zealand. J.R. Ottaway, September 1974. Extended length of slug 90 mm. From Ottaway, 1977b.

The view that cnidarians form a significant part of the natural diet of *Pleurobranchaea* species is further strengthened by my observations on *P. maculata* in New Zealand. I have seen *P. maculata* eating *Isactinia olivacea* (Actiniaria, Actiniidae) in the field (pers. obs., Leigh, May 1974). I have also collected a juvenile of this same species on buoy ropes so thickly covered with hydroids as to exclude all other organisms (pers. obs. Tataraimaka, Taranaki, May 1978). Cnidarians are certainly capable of supporting sustained growth and reproduction of *Pleurobranchaea* species in the laboratory in the absence of all other foods. In Australia, I have kept *P. maculata* alive for up to two months on a diet of *Actinia terebrosa* and in New Zealand I kept *P. maculata* in captivity on numerous occasions between 1974 and 1979. Specimens were maintained for up to four months and fed on actinians (mostly *Anthopleura aureoradiata*, sometimes *Isactinia olivacea* or *Actinia tenebrosa* or *Anthothoe albocincta*). On this diet the *Pleurobranchaea* grew naturally. When continually supplied with *Anthopleura aureoradiata*, *P. maculata* is capable of eating an average of 2.3 actinians per day (based on only two sets of observations; water temp. 8-14°C).

A hungry *Pleurobranchaea maculata* will actively seek food in daylight. This observation agrees with Davis and Mpitsos' (1971) findings that in *Pleurobranchaea californica* the urge to search for food suppressed the normal diurnal light response. In fact, recent experimental investigations have revealed a "behavioural hierarchy" in *Pleurobranchaea*, wherein certain important behaviours are superior or subordinate to others. Escape swimming dominates egg laying, which dominates feeding, which dominates righting, withdrawal and mating (Davis *et al.*, 1977). Therefore if a *Pleurobranchaea* is placed on its back and given food simultaneously it will ingest the food before righting itself; this observation, first made for *P. californica* (Davis *et al.*, 1974a), holds true for *P. maculata* (pers. obs.). The neurophysiological mechanisms underlying this "singleness of action" behaviour are being investigated intensively by Davis and co-workers (Davis *et al.*, 1973; 1974a; 1974b; Lee & Liegeois, 1974; Kovak & Davis, 1977; Siegler, 1977; Davis & Gillette, 1978; Gillette *et al.*, 1978). With appropriate ("avoidance") conditioning, *Pleurobranchaea* is capable of modifying its "behavioural hierarchy" (Mpitsos & Davis, 1973; Mpitsos & Collins, 1975; Davis *et al.*, 1977; Davis & Gillette, 1978). For example, starved animals have been trained (using a combination of food and electric shock) to suppress the feeding response and withdraw from food. The "behavioural hierarchy" of *Pleurobranchaea* can be modified directly by the influence of hormones; Ram and Davis (1977) discovered an egg-laying hormone (produced by the pedal ganglion) that causes inhibition of feeding.

Pleurobranchaea species apparently locate their food, at least over relatively great distances, by chemotaxis. In contrast to the report of Hirsch (1915), Lee *et al.* (1974) showed by controlled experiments that *Pleurobranchaea californica* could locate food from a distance. These authors found that crawling by an animal in response to food chemicals was not random, and that if the chemical gradient emanating from the food source was strong enough, animals consistently turned towards the food. They also investigated the location of chemical receptors (found mainly on the anterior border of the oral veil and foot, and rhinophoral tips) and satiation (which occurred after consumption of food equal to between five and ten per cent of body weight).

Lee and Palovcik (1976) defined states of activity to *Pleurobranchaea californica* with respect to stages of the feeding cycle. They found certain reflex actions of the body (responses to tactile stimuli) waned depending upon which state the subject was in. Changes in state were brought about by chemical or tactile stimulation.

The feeding behaviour of *Pleurobranchaea maculata* has not been fully reported previously. *P. maculata* exhibits the same behavioural sequence whenever food is encountered, and it consists of two phases. When the papillae that line the anterior edge of the oral veil contact a prey item, the stimulated region of the oral veil contracts at once (possibly as the result of stings by nematocysts if the prey is a cnidarian). At the same time the edges of the oral veil curve downwards to form a hemispherical

cup that prevents escape by any mobile organism. Almost instantaneously the oral tube is everted beneath the veil and thrust in the direction of the food stimulus. The rhinophores contract into the space between the oral veil and mantle. The jaws are at the tip of the oral tube and in this initial attack they come together with a grasping or clamping action.

Usually a single feeding lunge is sufficient to trap the prey, although the jaws themselves usually undergo several grasping cycles. Forward motion ceases, the anterior margin of the foot becomes embayed to surround the food from behind and on the sides, and the oral veil remains positioned above and in front of the prey (Fig. 6).

FIGS. 5, 6. Feeding behaviour of *Pleurobranchaea maculata*.

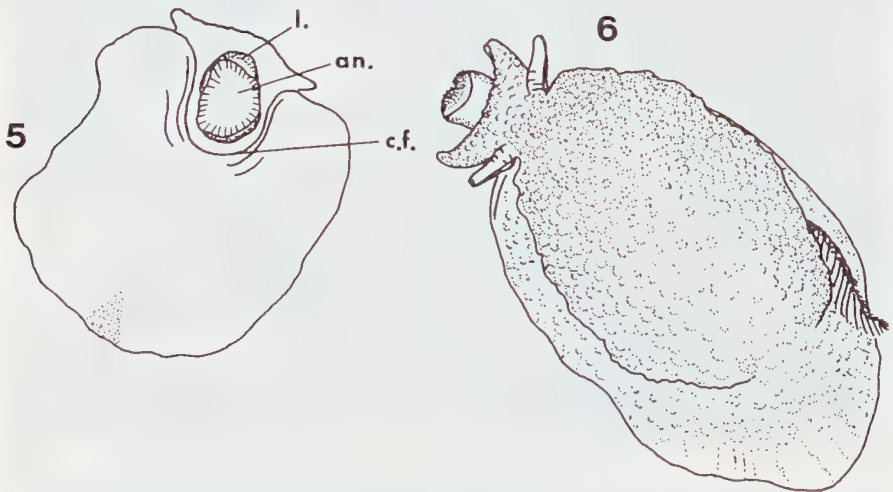


FIG. 5. Ventral view of specimen eating an actinian.

FIG. 6. Dorsal view of specimen making a feeding lunge.

Abbreviations: an. — pedicel of sea anemone; c.f. — crenulation in anterior margin of slug's foot; l. — lips.

With the prey thus surrounded, *Pleurobranchaea maculata* changes its position and feeding rhythm. The body flattens, the edges of the body and foot become outstretched with the mantle compressed against the foot on all sides. The anterior part of the body is raised so that the radula operates in a vertical plane (Fig. 5). The radula and jaws undergo regular, rhythmic cycles (about 10 per minute) as the slug rasps at the prey's tissues. Most often the rasping cycles are interrupted by pauses during which the oral tube remains partially protracted. After such a pause the slug may resume feeding with a few large grasping cycles by the jaws (similar to those produced on initial contact) before radular rasping resumes.

If the prey is small it is swallowed whole. The initial grasping cycles of the jaw are sufficient to ingest the prey without any trituration by the radula. On such occasions the jaws continue their grasping movements (though the rate of action is greatly slowed), and this results in a gulping action which takes in the prey.

The threshold of stimulation required to induce the initial feeding lunge (with oral veil cupping and proboscis protrusion) is extremely low. I have found this behaviour can be elicited by touching one of the papillae on the slug's oral veil with a single excised sea anemone tentacle (offered with forceps).

Items unacceptable to *Pleurobranchaea maculata* (such as algae, sponges, shelled molluscs, spicule-bearing opisthobranchs, opisthobranch spawn, echinoderms) cause rapid retraction of the oral veil immediately after contact. The foot then changes direction to avoid crawling over the organism. This rejection behaviour can occur with or without oral veil cupping. On occasions when it is extremely hungry, *P. maculata* will attack organisms with hard exoskeletons (e.g. gastropods, bivalves, crustaceans) but it leaves them after a feeding lunge.

Time for complete ingestion of large prey varies considerably, most continuous feeding bouts last between one and two hours. The mean time for *Pleurobranchaea maculata* to finish feeding on a single *Anthopleura aureoradiata* (about 10 mm basal diameter) was 74.18 min (standard deviation = 3.71 min, $n = 11$) (data averaged for three *P. maculata* with crawling lengths between 40 and 50 mm). In these trials, the *P. maculata* completely ingested the actinian upon which it was feeding in only six out of eleven trials; on the other occasions the animal crawled away before it had completely consumed the actinian. No correlation between time starved and feeding time was evident ($r = 0.026$).

Pleurobranchella

Members of this small genus apparently possess the same carnivorous habits as *Pleurobranchaea* (Willan, 1977). Eales (1937) found 14 juvenile *Pleurobranchaea capensis* in the stomach of one *Pleurobranchella gilchristi*. All known species of *Pleurobranchella* have been taken in deep water (>200,) so that the possibilities of direct feeding observations on any of them are remote.

Euselenops

I can find no references to feeding by *Euselenops luniceps*, the only species in the genus. It would be expected to be a voracious carnivore like *Pleurobranchaea* species because of the enlargement of the oral veil and because of its high level of activity (Pace, 1901).

SUMMARY

All the Umbraculacea have diets confined to sponges, with that of the genera *Tylodina* and *Tylodinella* apparently being narrowly restricted to a single demospongiid order (Verongida) and family (Aplysinellidae). That of *Umbraculum* is wider and consists of demospongiids belonging to at least two orders and three families. The same broad sponge diet is possessed by *Berthella* species, and there are no authenticated reports of members of this genus eating anything other than demospongiid sponges.

Bethellina species eat sponges but appear even more catholic in their choice. Not only do they take demospongiids, but calcareous sponges (class Calcarea) are also occasionally eaten as well. *Berthellina* species extend their diet beyond sponges to take cnidarians. In Hawaii, *B. citrina* has regularly been observed eating corals in the field. Since the corals presently known to be eaten by *B. citrina* belong to three scleractinian families, it is possible that in tropical waters *Berthellina* species eat a range of hermatypic corals as they do with sponges in temperate waters. Some (admittedly incomplete) tantalising evidence suggests *Berthellina* species may take ascidians or even meat.

Pleurobranchus species have only been found to eat ascidians. They accept both solitary and compound forms and are apparently not confined to one particular group of ascidians.

Pleurobranchaea species represent (in both their anatomy and feeding ecology) the culmination of the pleurobranch radiation. They are opportunistic carnivores with a low feeding specificity. They will attack and eat almost any live, soft-bodied invertebrate they encounter, although it appears they favour cnidarians. Hirsch (1915) suggested that some species are scavengers but subsequent literature has not supported his

contention. Despite Starmühlner's (1968) report, *Pleurobranchaea* species will not accept sponges or ascidians. Maybe these foods have been bypassed because they do not supply sufficient energy to maintain the fast, active life typical of *Pleurobranchaea* species?

In overview, it is evident that the Notaspidea displays an adaptive radiation of feeding habits. Primitive genera are restricted to sponges. Intermediate genera retain this diet but are capable of augmenting it with other foods. The most advanced genera accept a wide range of foods — virtually any soft-bodied invertebrate not protected by a shell or exoskeleton. Clark and Busacca (1978) have shown the same kind of radiation in another order of opisthobranchs, the Sacoglossa. All the species there are herbivorous, except for a very few of the most advanced ones which are oophagous (Chia & Skeel, 1973; Lemche, 1974).

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LITERATURE CITED

- Abbott, R.T., 1974. *American Seashells*. 2nd Ed. Van Nostrand Reinhold, New York. 663 pp.
- Ayling, A.L., 1978. *Population Biology and Competitive Interactions in Subtidal Sponge Dominated Communities of Temperate Waters*. Unpubl. Ph.D. thesis, University of Auckland. 113 pp.
- Barbour, M.A. 1979. A note on the distribution and food preferences of *Cadlina laevis* (Nudibranchia: Chromodorididae). *Nautilus* 93: 61-62.
- Beeman, R.D. and G.C. Williams, 1980. Opisthobranchia and Pulmonata: The Sea Slugs and Allies. Pp. 308-354. In: Morris, R.H., D.P. Abbot and E.C. Haderlie, *Intertidal Invertebrates of California*. Stanford University Press, California. 690 pp.
- Behrens, D.W., 1980. *Pacific Coast Nudibranchs*. Sea Challengers, California. 112 pp.
- Bergh, L.S.R., 1897. Die Pleurobranchiden — *Pleurobranchaea*. In: C.G. Semper, *Reisen im Archipel der Philippinen von Dr C. Semper, Malacologische Untersuchungen* 7(1): 1-51.
- 1898. Die Pleurobranchiden — *Pleurobranchus*. In: C.G. Semper, *Reisen im Archipel der Philippinen von Dr C. Semper, Malacologische Untersuchungen* 7(3): 117-158.
- Bergquist, P.R., 1978. *Sponges*. Hutchinson University Library, London. 268 pp.
- 1980. A revision of the supraspecific classification of the orders Dictyoceratida, Dendroceratida, and Verongida (class Demospongiae). *N.Z.J. Zool.* 7: 443-503.
- Bertsch, H., 1970. Opisthobranchs from Isla San Fransisco, Gulf of California, with the description of a new species. *Contributions in Science* (Santa Barbara Mus. Nat. Sci.) 2: 1-16.

- _____. 1980. A new species of Tyloidiidae (Mollusca: Opisthobranchia) from the north-eastern Pacific. *Sarsia* 65: 233-237.
- Bertsch, H. and S. Johnson, 1981. *Hawaiian Nudibranchs*. Oriental Publishing Co., Honolulu. 112 pp.
- Bouchet, P., F. Danrigal and C. Huyghens, 1978. *Coquillages des Côtes Atlantique et de la Manche*. Les Editions du Pacifique, Tahiti. 144 pp.
- Boury-Esnault, N., 1971. Spongiaires de la zone rocheuse de Banyuls-sur-Mer. II. Systématique. *Vie Milieu* 22: 287-350.
- Braams, W.G. and H.F.M. Geelen, 1953. The preference of some nudibranchs for certain coelenterates. *Arch. Néerl. Zool.* 10: 241-264.
- Brace, R.C., 1977. Shell attachment and associated musculature in the Notaspidea and Anaspidea (Gastropoda: Opisthobranchia). *Trans. Zool. Soc. Lond.* 34: 27-43.
- Burn, R., 1957. On some Opisthobranchiata from Victoria. *J. Malac. Soc. Aust.* 1(1): 11-29.
- _____. 1966a. Some opisthobranchs from southern Queensland. *J. Malac. Soc. Aust.* 1(9): 96-109.
- _____. 1966b. Opisthobranchia — Port Phillip Survey 1957-1963. *Mem. Nat. Mus. Vic.* 27: 265-288.
- Chamberlain, R. and D.W. Behrens, 1980. Deep water collections of opisthobranchs in central California. *Veliger* 22: 282-285.
- Chia, F.S. and M. Skeel, 1973. The effect of food consumption on growth, fecundity and mortality in a sacoglossan opisthobranch, *Olea hansineensis*. *Veliger* 16: 153-158.
- Chivers, D. D., 1967. Observations on *Pleurobranchaea californica* MacFarland, 1966 (Opisthobranchia, Notaspidea). *Proc. Calif. Acad. Sci.* 32: 515-521.
- Christensen, H., 1977. Feeding and reproduction in *Precuthona peachi* (Mollusca: Nudibranchia). *Ophelia* 16: 131-142.
- Clark, K.B. and M. Busacca, 1978. Feeding specificity and chloroplast retention in four tropical Ascoglossa, with a discussion on the extent of chloroplast symbiosis and the evolution of the order. *J. Moll. Stud.* 44: 272-282.
- Coan, E.V., 1964. A note on the natural history of *Pleurobranchaea* spec. (Gastropoda: Opisthobranchia). *Veliger* 6: 173.
- Conklin, E.J. and R.N. Mariscal, 1977. Feeding behavior, ceras structure and nematocyst storage in the aeolid nudibranch *Spurilla neapolitana*. *Bull. Mar. Sci.* 27: 658-667.
- Coleman, N., 1975. *What Shell is That?* Paul Hamlyn Pty Ltd, N.S.W. 308 pp.
- _____. 1981. *Shells Alive*. Rigby Publishers Ltd, Sydney. 96 pp.
- Davis, W.J. and R. Gillette, 1978. Neural correlate of behavioral plasticity in command neurons of *Pleurobranchaea*. *Science* 199: 801-804.
- Davis, W.J. and G.J. Mpitsos, 1971. Behavioral choice and habituation in the marine mollusk *Pleurobranchaea californica* MacFarland (Gastropoda, Opisthobranchia). *Z. Vgl. Physiol.* 75: 207-232.
- Davis, W.J., G.J. Mpitsos and J.M. Pinneo, 1974a. The behavioral hierarchy of the mollusk *Pleurobranchaea*. I. The dominant position of the feeding behavior. *J. Comp. Physiol.* 90: 207-224.

- Davis, W.J., G.J. Mpitsos, M.V.S. Siegler, J.M. Pinneo and K.B. Davis, 1974b. Neuronal substrates of behavioral hierarchies and associative learning in *Pleurobranchaea*. *Am. Zool.* 14: 1037-1050.
- Davis, W.J., G.J. Mpitsos, J.M. Pinneo and J.L. Ram, 1977. Modification of the behavioral hierarchy of *Pleurobranchaea*. II. Satiation and Feeding Motivation. *J. Comp. Physiol. A Sens. Neural Behav. Physiol.* 117: 99-125.
- Davis, W.J., M.V.S. Siegler and G.J. Mpitsos, 1973. Distributed neuronal oscillators and efference copy in the feeding system of *Pleurobranchaea*. *N. Neurophysiol.* 36: 258-274.
- Day, R.M. and L.G. Harris, 1978. Selection and turnover of coelenterate nematocysts in some aeolid nudibranchs. *Veliger* 21: 104-109.
- Delaloi, B. and J. Tardy, 1977. Régime alimentaire et ethologie predatrice de *Berthella plumula* (Montagu, 1803), mollusque, opisthobranch. *Halietis* 6 (for 1976): 273-280.
- Eales, N.B., 1937. Apparent viviparity in *Pleurobranchoides*. *Proc. Malac. Soc. Lond.* 22: 371-374.
- Edmunds, M.E., 1975. An aeolid nudibranch feeding on Bryozoa. *Veliger* 17: 269-270.
- Edmunds, M.E., G.W. Potts, R.C. Swinfen and V.L. Waters, 1974. The feeding preferences of *Aeolidia papillosa* (L) (Mollusca, Nudibranchia). *J. Mar. Biol. Assoc. U.K.* 54: 939-947.
- 1976. Defensive behaviour of some anemones in response to predation by the opisthobranch mollusc *Aeolidia papillosa* (L). *J. Mar. Biol. Assoc. U.K.* 56: 65-83.
- Elvin, D.W., 1976. Feeding of a dorid nudibranch, *Diaulula sandiegensis* on the sponge *Haliclona permollis*. *Veliger* 19: 194-198.
- Eyster, L.S. and S.E. Stanyck, 1981. Reproduction, growth and trophic interactions of *Doriopsilla pharpa* Marcus in South Carolina. *Bull. Mar. Sci.* 31: 72-82.
- Farmer, W.M., 1980. *Sea-slug Gastropods*. W.M. Farmer Enterprises Inc., Arizona. 177 pp.
- Garlo, E.V., 1977. Opisthobranchs found off Little Egg Inlet, New Jersey, with notes on three species new to the state. *Nautilus* 91: 23-28.
- Gillette, R., M.P. Kovak and W.J. Davis, 1978. Command neurons in *Pleurobranchaea* receive synaptic feedback from the motor network they excite. *Science* 199: 798-801.
- Gohar, H.A.F. and I.A. Abul-ela, 1957. The development of *Berthellina citrina* (Mollusca: Opisthobranchiata). *Publ. Mar. Biol. Stn. Al Ghardaga* 9: 69-83.
- Graham, A., 1955. Molluscan diets. *Proc. Malac. Soc. Lond.* 31: 144-159.
- Guiart, J., 1901. *Contributions à l'étude des gastéropodes opisthobranches et en particulier des céphalaspides*. Theses Presentees a la Faculte des Sciences de l'Université de Paris. Le Bigot Freres, Lille. 319 pp.
- Haefelfinger, H.T., 1962. Quelques faits concernant la nutrition chez *Favorinus branchialis* (Rathke, 1806) et *Stiliger vesiculosus* (Deshayes, 1864), deux mollesques opisthobranches. *Rev. Suisse Zool.* 69: 311-316.
- Hall, S.J., C.D. Todd and A.D. Gordon, 1982. The influence of ingestive conditioning on the prey species selection in *Aeolidia papillosa* (Mollusca: Nudibranchia). *J. Anim. Ecol.* 51: 907-921.
- Harris, L.G., 1973. Nudibranch associations. *Curr. Top. Comp. Pathobiol.* 2: 213-315.

- _____. 1975. Studies on the life history of two coral-eating nudibranchs of the genus *Phestilla*. Biol. Bull. (Woods Hole) 149: 539-550.
- Harris, L.G., L.W. Wright and B.R. Rivest, 1975. Observations on the occurrence and biology of the aeolid nudibranch *Cuthona nana* in New England waters. Veliger 17: 264-268.
- Hill, B.J., 1963. Contributions to the morphology and histology of the tectibranch *Berthella granulata* (Krauss). Ann. Univ. Stellenbosch Ser. A 38(5): 155-187.
- Hirsch, G.C., 1915. Die ernährungsbiologie fleischfressender gastropoden. Zool. Physiol. der Tiere 35: 357-504.
- Hoffmann, H., 1939. Pp. 1105-1247 In: BRONN, H.G., *Klassen und Ordnungen des Tierreichs. Opisthobranchia*. 3(2) Book 3. Akademische Verlagsgesellschaft, Leipzig. 1247 pp.
- Hunt, C.D., 1925. The food of the bottom fauna of the Plymouth fishing grounds. J. Mar. Biol. Assoc. U.K. 13: 560-598.
- Hyman, L.H., 1967. *The Invertebrates. Vol. 6. Mollusca I*. McGraw-Hill Book Co., New York. 792 pp.
- Kandel, E.R., 1979. *Behavioral Biology of Aplysia*. W.H. Freeman & Co., San Francisco. 463 pp.
- Kovak, M.P. and W.J. Davis, 1977. Behavioural choice: neural mechanism in *Pleurobranchaea*. Science 198: 632-634.
- Lacaze-Duthiers, H., 1859. Histoire anatomique et physiologique du pleurobranche orange. Ann. Sci. Nat. Zool. Biol. Anim. 11: 199-302.
- Lance, J.R., 1961. A distributional list of southern California opisthobranchs. Veliger 4: 64-69.
- Lee, R.M. and R.J. Liegeois, 1974. Motor and sensory mechanisms of feeding in *Pleurobranchaea*. J. Neurobiol. 5: 545-564.
- Lee, R.M. and R.A. Palovcik, 1976. Behavioral states and feeding in the gastropod *Pleurobranchaea*. Behav. Biol. 16: 251-266.
- Lee, R.M., M.R. Robbins and R.A. Palovcik, 1974. *Pleurobranchaea* behavior: food finding and other aspects of feeding. Behav. Biol. 12: 297-315.
- Lemche, H., 1974. Appendix (Pp. 124-126) to: Gascoigne, T. and P.K. Sartory, The teeth of three bivalved gastropods and three other species of the order Sacoglossa. Proc. Malac. Soc. Lond. 41: 109-126.
- MacFarland, F.M., 1966. Studies of opisthobranchiate mollusks of the Pacific Coast of North America. Calif. Acad. Sci. Mem. 6: 546 pp.
- McDonald, G.R. and J.W. Nybakken, 1978. Additional notes on the food of some California nudibranchs with a summary of known food habits of California species. Veliger 21: 110-119.
- Macnae, W., 1962. Notaspidean opisthobranchiate molluscs from Southern Africa. Ann. Natal Mus. 15(15): 167-181.
- Marbach, A. and M. Tsumamal, 1973. On the biology of *Berthellina citrina* (Gastropoda, Opisthobranchia) and its defensive acid secretion. Mar. Biol. (Berl.) 21: 331-339.
- Marcus, E., 1957. On Opisthobranchia from Brazil (2). J. Linn. Soc. Lond. Zool. 43: 390-486.

- Marcus, E. and E. Marcus, 1957. Sea-hares and side-gilled slugs from Brazil. *Bol. Inst. Oceanogr.* 6: 3-33.
- 1963. Opisthobranchs from the Lesser Antilles. *Stud. Fauna Curacao other Caribb. Is.* 19: 1-76.
- 1966. The R/V Pillsbury deep-sea expedition to the Gulf of Guinea, 1964-65. 9. Opisthobranchs from tropical West Africa. *Stud. Trop. Oceanogr. (Miami)* 4: 152-208.
- 1967. American opisthobranch mollusks. *Stud. Trop. Oceanogr. (Miami)* 6: 1-256.
- 1969. Opisthobranchian and lamellarian gastropods collected by the "Vema". *Am. Mus. Novit.* 2368: 1-33.
- 1970. Opisthobranch mollusks from the southern tropical Pacific. *Pac. Sci.* 24: 155-179.
- Mestayer, M.K., 1920. A note on *Pleurobranchaea novae-zelandiae* Cheeseman. *N.Z. J. Sci. Technol.* 3: 170.
- Minichev, Y.S. 1970. On the origin and system of nudibranchiate molluscs (Gastropoda Opisthobranchia). *Monit. Zool. Ital. (N.S.)* 4: 169-182.
- Minichev, Y.S. and Y.I. Starobocotov, 1978. On the systematic arrangement of euthyneuran snails. *Malacol. Rev.* 11: 67-68.
- Moore, G.M., 1964. Shell-less Opisthobranchiata. Pp. 155-164 *In*: Smith, R.I. (Ed.) *Keys to marine invertebrates of the Woods Hole Region. Contribution 11, System.* — *Ecol. Program Mar. Biol. Lab, Woods Hole.*
- Moquin-Tandon, C.H.B.A., 1870. Recherches anatomiques sur l'ombrelle du la Méditerranée. *Ann. Sci. Nat. Zool. Biol. Anim.* 14: 1-135.
- Morton, J.E., 1979. *Molluscs*. 5th Ed. Hutchinson, London. 264 pp.
- Morse, M.P., 1971. Biology and life history of the nudibranch mollusc, *Coryphella stimpsoni* (Verrill, 1879). *Biol. Bull. (Woods Hole)* 140: 84-94.
- Mpitsos, G.J. and S.D. Collins, 1975. Learning: rapid adverse conditioning in the gastropod mollusk *Pleurobranchaea*. *Science* 190: 954-957.
- Mpitsos, G.J. and W.J. Davis, 1973. Learning: classical and avoidance conditioning in the mollusk *Pleurobranchaea*. *Science* 180: 317-320.
- Nybakken, J.W., 1975. Phylum Mollusca: Gastropoda, Opisthobranchia. Pp. 515-542, *In*: SMITH, R.J. and J.T. Carlton (Eds), *Light's Manual: Intertidal Invertebrates of the Central California Coast* (3rd Ed.). University of California Press, Berkeley. 716 pp.
- Nybakken, J.W. and J. Eastman, 1977. Food preferences, food availability and resource partitioning in *Triopha maculata* and *Triopha carpenteri* (Opisthobranchia: Nudibranchia). *Veliger* 19: 279-289.
- Odhner, N.H., 1939. Opisthobranchiate Mollusca from the western and northern coasts of Norway. *K. Norse Vidensk. Selsk. Skv.* 7: 1-93.
- Ottaway, J.R., 1977a. Predators of sea anemones. *Tuatara* 22: 213-221.
- 1977b. *Pleurobranchaea novaezelandiae* preying on *Actinia tenebrosa*. *N.Z. J. Mar. Freshw. Res.* 11: 125-130.
- Pace, S., 1901. On the rediscovery of *Euselenops* (= *Neda*) *luniceps* (Cuv.). *Proc. Malac. Soc. Lond. (for 1901)*: 202-204.
- Perron, F.E. and R.D. Turner, 1977. Development, metamorphosis, and natural history of the nudibranch *Doridella obscura* Verrill (Corambidae: Opisthobranchia). *J. Exp. Mar. Biol. Ecol.* 27: 171-185.

- Potts, G.W., 1970. The ecology of *Onchidoris fusca* (Nudibranchia). J. Mar. Biol. Assoc. U.K. 50: 269-292.
- Pruvot-Fol, A., 1927. Sur queleques mollusques nudibranches de la côte atlantique du Maroc, récoltés principalement par MM. J. Liouville et R. Ph. Dollfus. Bull. Soc. Sci. Nat. Phys. Maroc 7: 39-49.
- 1954. *Mollusques Opisthobranches*. Faune de France 58. P. Le Chevalier, Paris. 460 pp.
- Ricketts, E.F. and J. Calvin, 1939. *Between Pacific Tides*. (1st Ed.). Stanford University Press, Stanford. 320 pp.
- Ram, J.L. and W.J. Davis, 1977. Mechanisms underlying "singleness of action" in the feeding behavior of *Pleurobranchaea californica* (MacFarland, 1966). Veliger 20: 55-56.
- Ros, J., 1975. Opisthobranquios (Gastropods: Euthyneura) del litoral ibérico. Invest. Pesq. 39: 269-372.
- Rudman, W.B., 1979. The ecology and anatomy of a new species of aeolid opisthobranch mollusc; a predator on the scleractinian coral *Porites*. Zool. J. Linn. Soc. 65: 339-350.
- 1981a. Further studies on the ecology and anatomy of opisthobranch molluscs feeding on the scleractinian coral *Porites*. Zool. J. Linn. Soc. 71: 373-412.
- 1981b. The anatomy and biology of alcyonarian-feeding aeolid opisthobranch molluscs and their development of symbiosis with zooxanthellae. Zool. J. Linn. Soc. 72: 219-262.
- Schmekel, L., 1968. Ascoglossa, Notaspidea und Nudibranchia in litoral des Golfes von Neapel. Rev. Suisse Zool. 75: 103-155.
- Seed, R., 1976. Observations on the ecology of *Membranipora* (Byrozoa) and a major predator *Doridella steinbergerae* (Nudibranchiata) along the fronds of *Laminaria saccharina* at Friday Harbour, Washington. J. Exp. Mar. Biol. Ecol. 24: 1-17.
- Siegler, M.V.S., 1977. Neuronal basis of *Pleurobranchaea* feeding. Veliger 20: 59-60.
- Sphon, G.C. and D.K. Mulliner, 1972. A preliminary list of known Opisthobranchs from the Galapagos Islands collected by the Ameripagos Expedition. Veliger 15: 147-157.
- Starmühlner, F., 1968. Investigations about the mollusc fauna in submarine caves. Proc. Symp. Mollusca 1: 136-163.
- Steehouwer, H., 1955. The preference of the slug *Aeolidia papillosa* (L.) for the sea anemone *Metridium senile* (L.). Arch. Néerl. Zool. 10: 162-170.
- Strasburger, E., 1879. Wirkung des Lichtes und der Wärme auf Schwarmsporen. Z. Naturw. (Jena) 12: 551-625.
- Thompson, T.E., 1970. Eastern Australian Pleurobranchomorpha (Gastropoda, Opisthobranchia). J. Zool. (Lond.) 160: 173-198.
- 1976. *Biology of Opisthobranch Molluscs*. Vol. 1, Monograph No. 151. The Ray Society, London 297 pp.
- 1977. Jamaican opisthobranch molluscs I. J. Moll. Stud. 43: 93-140.
- Thompson, T.E. and G.H. Brown, 1976. British opisthobranch molluscs. Mollusca. Gastropoda. Keys and notes for the identification of the species. Synopses British Fauna (N.S.) 8: 203 pp.
- Thompson, T.E. and D.J. Slinn, 1959. On the biology of the opisthobranch *Pleurobranchus membranaceus*. J. Mar. Biol. Assoc. U.K. 38: 507-524.
- Truman, J.W., 1978. Hormonal control of invertebrate behaviour. Horm. Behav. 10: 214-234.
- Usuki, I., 1969. The reproduction, development and life history of *Berthellina citrina* (Rüppell & Leuckart) (Gastropoda, Opisthobranchia). Sci. Rep. Niigata Univ. Ser. D. Biol. 6: 107-127.
- Vayssière, A., 1883. Recherches anatomiques sur les genres *Pelta* (*Runicina*) et *Tylodina*. Ann. sci. Nat. (Zool. Paleontol) 6(15) No. 1: 1-46.
- 1898. Monographie de la famille des Pleurobranchidés I. Ann. Sci. Nat. Zool. Biol. Anim. 8(8): 209-402.
- 1901. Monographie de la famille des Pleurobranchidés (Deuxième et dernière partie). Ann. Sci. Nat. Zool. Biol. Anim. 8(12): 1-85.

- Willan, R.C., 1975. *Identity and feeding of New Zealand notaspidean opisthobranchs (Mollusca: Gastropoda)*. Unpubl. M.Sc. thesis, University of Auckland, 164 pp.
- 1977. A review of *Pleurobranchella* Thiele, 1925 (Opisthobranchia: Pleurobranchaeinae). *J. Conchol.* 29: 151-155.
- 1984. New Zealand side-gilled sea slugs (Opisthobranchia: Notaspidea: Pleurobranchidae). *Malacologia* 23: 221-270.
- Willan, R.C. and J.E. Morton, 1983. *Marine Molluscs Part 2 — Opisthobranchia*. University of Auckland, Leigh Marine Laboratory. 106 pp.
- Yonge, C.M., 1949. *The Sea Shore*. Collins, London. 311 pp.
- Yonge, C.M. and T.E. Thompson, 1976. *Living Marine Molluscs*. Collins, London. 288 pp.